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SURFACE TOPOGRAPHY INFLUENCES COMPETITIVE HIERARCHIES ON MARINE HARD SUBSTRATA: A FIELD EXPERIMENT

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ABSTRACT

Among colonial encrusting organisms, competitive relations often are intransitive, with individuals of subordinate species occasionally winning encounters with higher ranking species. Many mechanisms, including allelopathy, growth form, and disturbance have been proposed to explain this phenomenon. We show experimentally that such reversals of rank can occur purely as a result of surface topography. The bryozoan *Alcyonidium* was superior to the bryozoan *Electra* when encounters occurred on level substrata (8 wins, 0 losses). When *Electra* was given a 1.6 mm height advantage in the zone of contact, it won in 15 out of 16 encounters with *Alcyonidium*. This mechanism may explain the higher incidence of intransitivity among epifauna on the topographically variable *Fucus serratus* in Wales, compared to the competitive hierarchy seen on the topographically more uniform *Fucus distichus* ssp. *evanescens* and *Chondrus crispus* in New England.

INTRODUCTION

On space-limited natural and artificial marine hard substrata, interference competition via overgrowth is common (*e.g.,* Jackson and Buss, 1975; Jackson, 1979; Paine, 1984; Sebens, 1986). In most pairwise interspecific interactions, one species more frequently overgrows the other (*i.e.,* species A > species B in greater than 50% of the interactions). When pairwise interactions among all species are taken together— especially when different phyla are compared—the ranking of competitors appears hierarchical and mathematically transitive (A > B > C and A > C). In the absence of predation or disturbance, the rate at which the competitively dominant species eliminates subordinate species depends upon: (1) the frequency of interspecific contacts, (2) species-specific rates of recruitment into the system, (3) relative growth rates of species, and (4) the degree of asymmetry in interspecific competitive outcomes (*i.e.,* species A may not always overgrow species B). The less the certainty that species A will overgrow species B in a given interaction (and the greater the possibility of a competitive reversal in which species B actually overgrows species A), the slower the rate at which species A will monopolize space.

Although some authors consider reversals to be intransitivities (*e.g.* A > B > C and C > A) averaged over all interactions among three or more species, here reversals will be defined in terms of individuals. A reversal will be defined as any instance in which an individual of a subordinate species overgrows an individual of a dominant species. Using this definition, reversals play a small role in the maintenance of diversity if they are rare, but if they occur frequently, then they may be very important.

A variety of mechanisms have been proposed to explain competitive reversals in colonial organisms in the intertidal and subtidal. These include differences in the size

of individual combatting colonies (Day, 1977; Buss, 1980, 1981; Russ, 1982), encounter angle between colonies (Jackson, 1979; Buss, 1981; Rubin, 1982), allelochemical interactions (Jackson and Buss, 1975; Green, 1977; Jackson, 1979; Stoecker, 1980), differences in the growth form of competitors (Jackson, 1979; Buss, 1980, 1981), the influence of grazers and/or disturbance agents (Paine, 1984), and surface topography (Paine, 1984; Connell and Keough, 1985).

Three mechanisms involving vertical relief influence the outcomes of competitive interactions in epifaunal systems. First, the thicker of the two colonies usually wins (Buss, 1980; Seed and O'Connor, 1981; Russ, 1982; Sebens, 1985, 1986). This has been demonstrated in many communities with thick, fleshy organisms, such as the bryozoan *Flustrellidra* or the ascidian *Botryllus,* overgrowing much thinner species, such as *Electra* (LJW, per. obs.). Colony thickness, hence competitive ability, may not be a fixed species-specific trait, but dependent on the colony's age (Buss, 1980, 1981). Buss (1981) showed how one tropical cheilostome bryozoan species became thicker as it grew larger, thereby enhancing its competitive ability. Second, colonies may be able to elevate their growing edges over competitors thereby blocking overgrowth or overgrowing the competitor themselves (*e.g.,* frontally budding bryozoans such as *Schizoporella*) (Jackson and Buss, 1975; Buss and Jackson, 1979; Jackson, 1979). Third, the colonies occupying topographic highs may have a competitive advantage. Paine (1984) noted that certain coralline algal species, such as *Lithophyllum,* tend to occupy topographic highs, rendering overgrowth more difficult. Species located on the high spots of a topographically heterogeneous substrata may also be at an initial competitive advantage (Connell and Keough, 1985).

The work presented here is an experimental test of the hypothesis that differences in the elevation of the growing edges of interacting colonies cause reversals in a competitive hierarchy in a temperate epifaunal community. The outcome of competitive interactions between two species was reversed by changing the colony elevation at the point of contact. These results are compared to the patterns of overgrowth in epifaunal species growing on algal substrata in various locations throughout the year.

MATERIALS AND METHODS

Live colonies of the ascidian *Botryllus schlosseri* and the bryozoans *Electra* and *Alcyonidium* were collected on algae and on strips of plastic suspended from buoys in Long Island Sound at the Yale Peabody Museum Field Station, Guilford, Connecticut (41°16′N, 72°44′W), from June to August, 1984. Small pieces of algae containing an entire bryozoan colony were glued onto 2.5 cm × 7.5 cm × 1.6 mm pieces of clear acrylic plastic using cyanoacrylate glue. Stocks of *Botryllus* were maintained in a running seawater tank. When needed, *Botryllus* zooids were cut from the parent colony through the tunic with a razor blade and placed on clear acrylic in petri dishes kept moist with damp paper towels for approximately six hours. During this time the zooids attached to the new substrata (Grosberg, per. com.). Colonies of both phyla were kept in the running seawater tank for several days to ensure their viability. Only colonies of *Botryllus* that had budded at least once and bryozoans that still had functioning lophophores were used. Colonies were then suspended two meters beneath a raft in the 25°C waters of Long Island Sound in clear plastic slide boxes, open on both sides. Experiments were run from 12 July to 8 September. After bryozoan colonies had grown off the edge of the algae and onto the slide, competitive bouts between all viable colonies were set up. Every effort was made to make sure the growing edges of the two colonies would meet (frontal encounter, *sensu* Jackson, 1979) and to use colonies of approximately the same area. Level encounters, with both competitors in the same

plane, and raised edge encounters, with one slide glued (with cyanoacrylate glue) above the edge of another (1.6 mm height difference) were randomly prepared and run simultaneously from 21 July to 8 September (Fig. 2). They were suspended from the raft in open slide boxes and examined every two days. Colony overgrowth was scored as a win when one species overgrew another for at least a ten-day period. At this point the superior organism often occupied at least 70% of both slides.

The outcomes of the experimental competitive interactions were compared to the pattern of interactions for common, encrusting, colonial species on natural algal sub-strata found in the low intertidal zone. The abundance, distribution, and overgrowths (defined as the occlusion of at least one zooid by the overgrowing colony, *e.g.,* Stebbing, 1973b) of epifauna were scored using a dissecting microscope. Measurements were made on *Fucus serratus* in North Wales in the spring of 1982, on *Fucus distichus* ssp. *evanescens* in northern New England (Harpswell, Maine, and Durham, New Hamp-shire) in the fall of 1982 and on *Chondrus crispus* on Horse Island in Long Island Sound during the summer of 1984 while the experiment was running. Although these measures are static and may not represent the final outcome of all pairwise competitive encounters (Ayling, 1983; Keough, 1983, 1984), hierarchies are apparent. All data were tabulated as win-loss matrices (*e.g.,* Jackson and Buss, 1975; Osman, 1977; Russ, 1982; Paine, 1984). An overgrowth index was calculated by dividing the number of wins for each species by the number of encounters in which the species was involved (Taylor, 1979; Rubin, 1982). The index is a measure of competitive ability. Diagrams show where hierarchies exist.

We define the "dominant" in the pairwise interactions to be the species that wins more than 50% of its encounters. "Consistency" of the outcome of a particular pairwise interaction is defined as the percentage of encounters in which the "dominant" species wins. "Reversals" of competitive outcomes, scored on an individual basis, thus con-tribute to reduced "consistency" (or greater "ambiguity") of outcomes on a popula-tion basis.

RESULTS

Field experiments

When species competed on level surfaces, outcomes were hierarchical (Fig. 1A). *Botryllus* overgrew *Alcyonidium* in eight out of eight encounters and *Electra* in 11 out of 11 encounters (Fig. 1A). In turn, *Alcyonidium* overgrew *Electra* in all cases (Fig. 1A), suggesting that competitive relationships between the three species are completely transitive (B > A > E & B > E). However, where *Electra* had a height advantage at the contact margin, it won 15 of 16 encounters with *Alcyonidium* (Fig. 1B). This is a reversal of ranks of *Electra* and *Alcyonidium.* This reversal of rank, dependent on elevation, is evident in the events that occurred on one of our plates (Fig. 2). *Electra* with a 1.6 mm height advantage overgrew the *Alcyonidium* beneath it (Fig. 2C, D). However, on the right hand side of the slide, *Alcyonidium* grew up onto the top slide and there on the level it overgrew *Electra.* It could be argued that the results are confounded in counting a level and an edge interaction for the same pair of colonies because feeding currents are shared and there may be a reaction to the interaction that occurred first. However, this is really the best test of the hypothesis, seeing the outcome reversed in the same colonies with a height change. Figures 2C, D, and E show a unique case in which a third competitor, a *Botryllus* colony, settled on the back of the slide, and grew around to the front. It then overgrew both *Electra* and *Alcyonidium* (Fig. 2C, E).
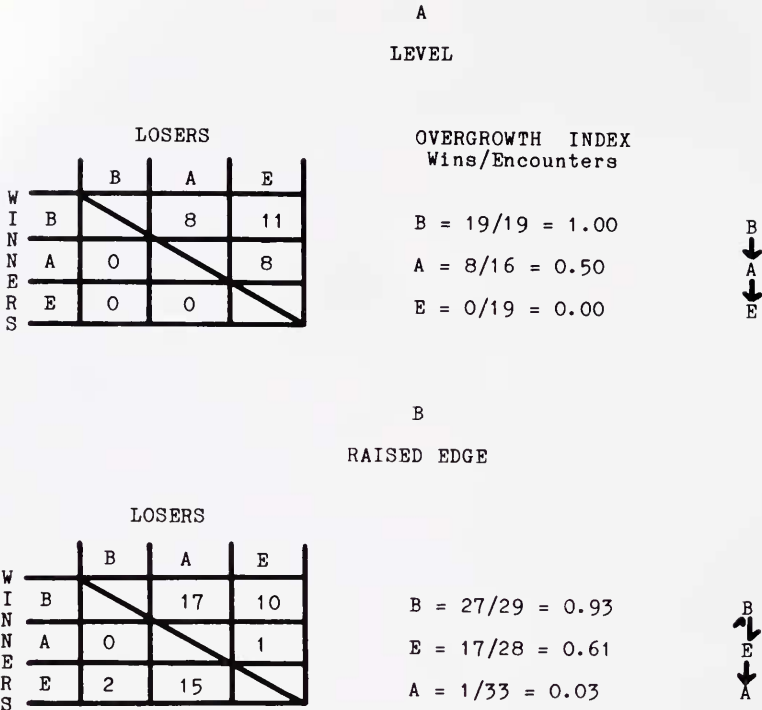
A

LEVEL

LOSERS   OVERGROWTH INDEX
                                    Wins/Encounters

	B	A	E
W I N N E R S B	╲	8	11
A	0	╲	8
E	0	0	╲

B = 19/19 = 1.00   B
                        ↓
A = 8/16 = 0.50   A
                        ↓
E = 0/19 = 0.00   E

B

RAISED EDGE

LOSERS

	B	A	E
W I N N E R S B	╲	17	10
A	0	╲	1
E	2	15	╲

B = 27/29 = 0.93   B
                        ↑↓
E = 17/28 = 0.61   E
                        ↓
A = 1/33 = 0.03   A

FIGURE 1. The outcome of experimental competitive interactions. Numbers in the arrays show the overgrowths seen in pairwise competitive interactions for species on A: level clear plastic surfaces and B: plastic surfaces with a raised edge. Taxa involved include B—*Botryllus,* A—*Alcyonidium,* and E—*Electra.* The winners are listed in the rows of each table and the losers in the columns. For example, on the level, *Botryllus* beat *Alcyonidium* eight times and never lost to it. The second column shows the ratio of wins to total number of encounters for each species (overgrowth index). This provides an index of each species' competitive rank in that system. The diagramed competitive rankings show this ordering. If the overgrowth index in a particular pairwise interaction is greater than 10:1, single-headed arrows are used, pointing to the subordinate species. If the win/encounter ratio is less than 10:1, arrows are drawn in each direction proportional to the ratio.

On substrata where *Botryllus* was at a lower elevation than *Electra* or *Alcyonidium,* during initial frontal encounters, both *Electra* and *Alcyonidium* appeared to overgrow *Botryllus* for up to four days (Fig. 3D). Subsequently, *Botryllus* overgrew most competitors (25 of 27 interactions, Fig. 1B) by flanking the competitor on the higher plane (Fig. 3E, F). Within six days of the initial encounter, *Botryllus* overgrew most competitors from the sides. In all occurrences of intraspecific *Botryllus* interactions (11 level encounters, 5 raised edge encounters), the colonies apparently fused.

Natural algal substrata

Epifaunal coverage exceeded 90–100% of the area of some *Fucus serratus* in North Wales. A hierarchy of competitive ability appears to exist, although many ambiguities are seen in the outcomes of encounters (Fig. 4A). The consistency of competitive outcomes was varied from a high of 93% (between *A. polyoum* and *A. hirsutum*) to a low of 65% (between *Celleporella* and *Electra.* Overall, the consistency of outcomes was 81%. Fewer encrusting species are common in Maine and New Hampshire (Fig.
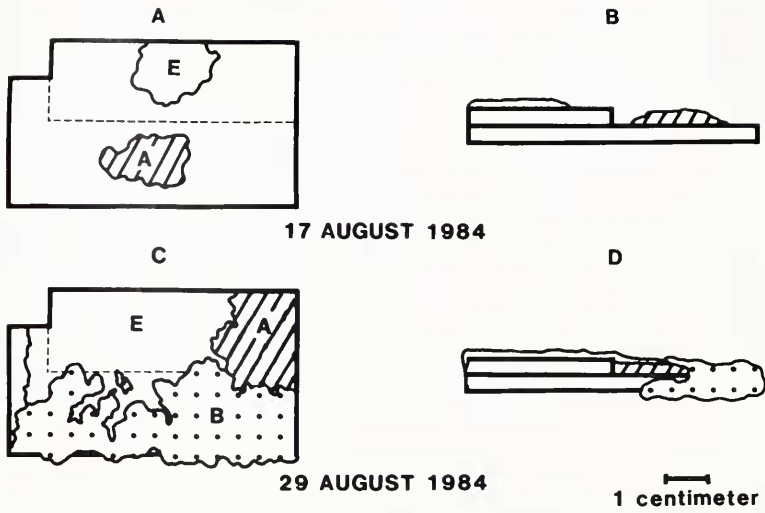
FIGURE 2. An example of a raised edge competitive interaction. Drawings were made by tracing photographs (taken with a Nikonos 35 mm camera fitted with a 2:1 extension ring) of the colonies' outlines on to tracing paper using a light table. In A and B, *Electra* (E) and *Alcyonidium* (A) are shown at the start of the experiment on August 17. In C and D, 12 days later, *Electra* with a 1.6 mm height advantage has grown over the *Alcyonidium* beneath it. However, a portion of the *Alcyonidium* colony escaped overgrowth long enough to invade the higher surface. On the level, *Alcyonidium* is overgrowing the *Electra* colony. A *Botryllus* colony (B), that settled on the back of the lower slide, has grown around to the front and is overgrowing both *Electra* and *Alcyonidium*. E is the photo from which C was taken.
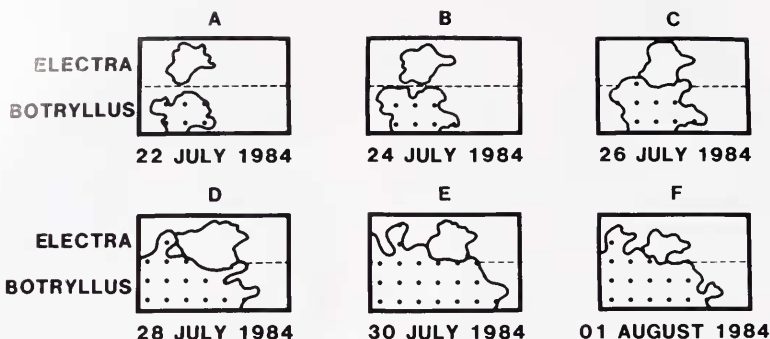
FIGURE 3. *Botryllus* defense when initially losing in a competitive bout with a height disadvantage. Long tunic arms grow over onto the higher slide. Within days it overgrows its competitor on the level at the flanks.

4B). A hierarchy is more apparent here and it is similar to that found in Long Island Sound (Fig. 4C). In Maine and New Hampshire, and in Long Island Sound, four out of five pairwise interactions had greater than 99% consistency of outcomes. Two of the species, *Electra* and *Membranipora,* rarely interact because their seasons of maximum abundance differ. In all observations on algal substrata, *Alcyonidium* dominates *Electra* (Fig. 4).

DISCUSSION

Although the outcomes of competitive interactions are often assumed to be independent of environmental conditions, a number of recent studies contradict this assumption. This study examined the influence of elevation differences on competitive rankings of species in an epifaunal community. Where colonies interacted on a level surface, a completely transitive competitive hierarchy resulted with *Botryllus* overgrowing both *Alcyonidium* and *Electra,* and *Alcyonidium* overgrowing *Electra.* Even where *Botryllus* was at an initial height disadvantage with respect to *Alcyonidium* and *Electra,* it continued to be the dominant overgrowth competitor by quickly flanking the other individual on the higher surface (Fig. 1B). In contrast, when *Electra* was elevated with respect to *Alcyonidium,* it overgrew *Alcyonidium* in 15 of 16 contacts (Fig. 1B). This suggests that colony elevation is an important determinant of the outcomes of encounters between encrusting bryozoans.

The results of this experiment contrast with those of coralline algae on topographically heterogenous substrata and smooth surfaces (Paine, 1984). On natural rough substrata with grazers, Paine (1984) found the outcomes of pairwise encounters to be 80% consistent; on natural rough surfaces with herbivores excluded, outcomes were 96% consistent; and on smooth, ungrazed surfaces, outcomes were 97% consistent. The results suggest that the presence of grazers increases the ambiguities in the outcomes of encounters on "natural" substrata. In *Lithothamnion,* for example, the ratio of wins to losses changed in the presence of grazers. The effects of grazing are unclear on smooth surfaces. In the absence of herbivory, topography introduces little ambiguity in the outcomes of interactions in these coralline algae. Paine (1984) notes however that survival of *Lithophyllum* is enhanced by occupying topographic highs, thus rendering its overgrowth by *Pseudolithophyllum* more difficult, suggesting that even in this system topography is important. In the present experiment, with no apparent predation, differences in colony elevation at the contact margin did cause reversals of

A

NORTH WALES

LOSERS

WINNERS	F	Ah	Ap	E	C
F		1	5	123	8
Ah	3		14	107	0
Ap	2	1		34	5
E	23	17	11		30
C	2	0	4	16	

OVERGROWTH INDEX
Wins/Encounters

Ah = 124/143 = 0.87

F = 137/167 = 0.82

Ap = 42/76 = 0.55

C = 22/65 = 0.34
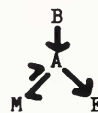
E = 81/361 = 0.23

B

MAINE & NEW HAMPSHIRE

LOSERS

WINNERS	B	A	E	M
B		2	16	5
A	0		258	2
E	0	1		0
M	0	1	0	

B = 23/23 = 1.00

A = 260/264 = 0.99

M = 1/8 = 0.13

E = 1/275 = 0.00

C

CONNECTICUT

LOSERS

WINNERS	B	A	E	M
B		27	10	12
A	5		22	171
E	0	2		0
M	0	1	1	

B = 49/54 = 0.91

A = 198/228 = 0.87

E = 2/35 = 0.06

M = 2/185 = 0.01
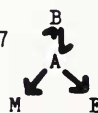
FIGURE 4. The outcome of competitive interactions on natural substrata. Numbers in the arrays show the overgrowths seen in pairwise competitive interactions for species on A: North Wales, B: Maine and New Hampshire and C: Long Island Sound. Species included are F—*Flustrellidra hispida*, Ap—*Alcyonidium polyoum*, Ah—*Alcyonidium hirsutum*, E—*Electra pilosa* and C—*Celleporella halina*, B—*Botryllus schlosseri*, A—*Alcyonidium* sp., and M—*Membranipora membranacea*. The notations used are the same as in Figure 1.

outcomes in competition. Either the two systems are substantially different or on Paine's (1984) natural, ungrazed surfaces, lower ranking species were not present on high spots.

Differences in topographic complexity may explain the lower consistency of outcomes of interspecific encounters and increased species diversity in the natural epifaunal

assemblege in Wales *versus* the northeastern United States. In Wales, the epifauna are growing on *Fucus serratus,* which has surface relief in the form of a thick midrib. The American data, which are more hierarchical, were collected on algae (*Fucus distichus* and *evanescens* and *Chondrus crispus*) that have very little surface relief. Similarly, Fletcher and Day (1983) showed greater epifaunal species diversity on crinkled than on smooth *Laminaria* plants. Thus the comparison of topographically simple and complex habitats conforms to the predictions from our experiment.

If there are spatial refuges from competition, selection should favor larvae that preferentially settle in those refuges, or colonies that grow towards refuges after settlement (*e.g.,* Buss, 1979). Topographic highs are local temporary refugia from competition (*e.g.,* Fig. 1), but contrary to expectation, larvae apparently do not settle preferentially on them. Several species are rugophilic, but settle in depressions (not topographic highs) on crinkly algae or the troughs along the midrib of *Fucoid* algae (*e.g.,* Crisp and Williams, 1960; Eggleston, 1972; Ryland, 1976; Berstein and Jung, 1979). Settlement behavior and colony growth in relation to topography merit further study.

Alternative mechanisms that promote coexistence include growth form changes and avoidance of competitors at the time of larval settlement. The polychaete *Spirobis* can reorient its tube angle to grow above a competitor (Stebbing, 1973b). *Electra* has been shown to produce spines at the margin of contact which reduces the rate of overgrowth (Stebbing, 1973a). Several taxa of marine invertebrates avoid settling on substrata where there is a high probability of death from a superior spatial competitor (*e.g.,* Grosberg, 1981; Young and Chia, 1981).

A number of mechanisms (*e.g.,* density and size-dependent competitive ability, predation, physical disturbance, habitat selection, etc.) have been proposed to explain the maintenance of diversity in space-limited marine epibenthic communities. Any process which either decreases the likelihood of an encounter between a dominant and a subordinate species, or increases the likelihood of a normally subordinate species surviving (or even winning) such an encounter, should act to slow the rate at which diversity is lost from the system. Our results show that subordinate species may obtain an elevation-dependent competitive advantage or temporal refuge from competition in a topographically complex environment.

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